# Genetic Diversity and Agronomic Improvement of North American Soybean Germplasm

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**ABSTRACT**

From 1970 to 2008 there were 2242 soybean [*Glycine max* (L.) Merr.] cultivars registered in North America through U.S. Plant Variety Protection (PVP), U.S. utility patent, and journal registration. Of these, 80% were developed through proprietary and 20% through public programs. Our objective was to characterize the development and genetic diversity of North American soybean cultivars. The most frequently used germplasm for cultivar development were the cultivars Williams (parent used in last cross before inbreeding in 70 cultivars), A3127 (63), Essex (45), Amsoy (38), Corsoy (33), Wayne (30), Forrest (27), Hutcheson (25), MO13404 (23), and Bedford (23). Genetic diversity (1 – coefficient of parentage), estimated from pedigree lineage, was 0.89 overall. Genetic diversity was the same within public (0.89) and proprietary (0.89) cultivars. The cultivar A3127 is a major progenitor of recently developed proprietary cultivars registered from 1999 to 2008. Of these 494 cultivars, 23% have a genetic contribution of at least 25% from A3127. New cultivars were predominantly developed from the following crosses: two-parent (70% of cultivars developed), complex (12%), three-parent (5%), one backcross (5%), multiple (two, three, or four) backcrosses (3%), and five or greater backcrosses (2%). In comparisons where both parent and progeny were evaluated together, seed yield increased 3.2% per breeding cycle. In these comparisons, seed yield had a correlation of 0.29 with parental diversity.

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**Abbreviations:** CP, coefficient of parentage; MG, maturity group; PVP, Plant Variety Protection.

Corn (*Zea mays* L.) and soybeans [*Glycine max* (L.) Merr.] are the most widely grown field crops in the United States, with 35.3 and 30.2 million planted hectares in 2008, respectively (NASS, 2008). The germplasm base of these crops is rapidly transitioning from public to proprietary origin. Nearly all North American commercial inbred corn lines and soybean cultivars are developed and marketed by private companies (IASS, 1998; Mikel and Dudley, 2006; NDASS, 2003; Sneller, 1994).

Genetic diversity of field crops is reduced by the frequent practice of plant breeders recycling a small subset of elite commercial varieties each breeding cycle. Criteria for germplasm selection are predominantly based on agronomic merit rather than maintaining or introducing new diversity. This breeding strategy is used because experience has demonstrated that the recombination of elite germplasm increases the probability of developing improved progeny. Unfortunately, over time this approach will lead to a narrowing genetic base in the absence of the introduction of new sources of diversity. Conversely, it is widely viewed that selection

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and breeding on the sole basis of expanding genetic diversity will at least temporarily slow gain per breeding cycle (Smith et al., 1999). In soybean, genetic diversity can be improved by increasing the mix of exotic and unrelated germplasm into breeding programs, while still maintaining the productivity of recycling elite cultivars (Thompson and Nelson, 1998; Warburton et al., 2004).

In dent corn, Mikel and Dudley (2006) determined that most contemporary North American hybrids share ancestry with at least one of eight inbred progenitors. Similarly, North American soybean cultivars descend from a small set of ancestors. Gizlice et al. (1994) found that 95% of the genes in cultivars released between 1947 and 1988 traced back to 35 genotypes. Sneller (1994) determined that breeders' efforts to expand the genetic diversity of soybeans have not succeeded.

Little is known about the genetic makeup and diversity of North American proprietary soybean germplasm that currently dominates production in farmers' fields. The registration of proprietary cultivars through Plant Variety Protection (PVP) and U.S. utility patent allows access to pedigree, phenotypic description, and agronomic performance. This study summarizes this information on both public and proprietary soybean cultivars registered from 1970 to 2008. The main objectives of our study were to identify the key progenitor cultivars of U.S. soybean germplasm and to estimate both genetic diversity and agronomic gain per breeding cycle during this era.

## MATERIALS AND METHODS

The breeding history of registered soybean cultivars for the years 1970 to 2008 was determined through analysis of U.S. utility patents, U.S. PVP certificates, and registration articles in the journals *Crop Science* and *Canadian Journal of Plant Science*. Parental lineage was traced as far back as possible. Time of registration was determined as year of patent application, PVP application, or year of journal publication. Plant Variety Protection and utility patent applications that were withdrawn, abandoned, or not granted remain sealed to the public and could not be used in this study. Typically, there is a hiatus of several years between patent or PVP application and the publication of the PVP certificate or patent. Utility patents do not require publication of cultivar breeding history, but PVP and journal publications do. Pedigree information in cultivar patents is generally available because most have their pedigree exhibited in the patent and/or are dual registered by PVP.

Registration publications were surveyed and summarized for ownership, media of registration, year of registration, pubescence color (gray or tawny), pod color (brown or tan), flower color (purple or white), herbicide tolerance (ALS [acetolactate synthase], glyphosate, or none), growth habit (determinate, semi-determinate, or indeterminate), and maturity group (MG) (00, 0, I, II, III, IV, V, VI, VII, VIII, IX, or X). Type of cross used in the development of each registered cultivar was classified as either two-parent, three-parent, one backcross (BC1), BC2 through BC4, BC5 or greater, broad base, complex cross, induced mutation, or selection within a cultivar. A complex cross is defined as a series of crosses involving more than three different cultivars or breeding lines. Cross type was summarized over all cultivars registered during this era (1970 through 2008), during decade subsets (1970–1979, 1980–1989, 1990–1999, and 2000–2008) within the era, and for public versus proprietary cultivars.

Publicly developed cultivars are listed with standard nomenclature. Proprietary cultivars are designated with the following prefixes: Asgrow (A), Delta Pine and Land (DP), Midwest Oilseeds (MO), Pioneer Hi-Bred (P), and Syngenta (S). Midwest Oilseeds is affiliated with Stine Seeds (ST). Throughout this text, cross will indicate hybridization or breeding cross used for development of new cultivars. Key germplasm was identified, similar to Mikel and Kolb (2008), by summing the number of times a cultivar was used as a parent in the last cross before inbreeding. Once identified, these popular parental cultivars were summarized over the entire era (1970–2008), during decade subsets (1970–1979, 1980–1989, 1990–1999, and 2000–2008) of the era, and public versus proprietary programs.

KIN (Tinker and Mather, 1993) software was used to calculate coefficient of parentage (CP), and from this a pedigree-based estimate of genetic diversity (1 − CP) was calculated between all cultivar pairs registered from 1970 through 2008 (Mikel, 2008). Values for genetic diversity range from 0 to 1, with 0 indicating no diversity and 1 indicating maximum diversity. These values were summarized among MGs and among publicly and proprietary developed cultivars. Coefficient of parentage is the probability that two alleles at a randomly selected locus are identical by descent. The following assumptions were used in calculating genetic distance: (i) progeny inherit genes equally from both parents, (ii) parents are homozygous, (iii) parental ancestors with unknown pedigrees are unrelated, and (iv) BC5 or greater derived isolines are considered identical to the recurrent parent (Martin et al., 1991; Sneller, 1994; Van Beuningen and Busch, 1997; Wang and Lu, 2006). A caveat to using CP is the assumption that parental (founder generation) ancestors with unknown pedigrees are unrelated. The founder generation, though not linked by pedigree, likely has an undetermined number of genes that are identical by descent from remote ancestors. Thus, the CP between two lines is most likely an underestimate of the number of loci that are identical by descent and conversely an overestimate of genetic diversity (1 − CP). To determine genetic diversity of the 38 cultivars most used as parents in last cross before inbreeding from 1970 to 2008, a dendrogram was constructed using unweighted pair group method analysis (UPGMA) in the SAHN program within NTSYSpc (Rolf, 2007) using genetic diversity (dissimilarity, 1 − CP) between all cultivar pairs.

Genetic contribution of key progenitors to contemporary (1999 through 2008) registered proprietary soybean cultivars was calculated. The genetic contribution of a progenitor to these cultivars consisted of the theoretical portion of genes that traced back to each progenitor (Delannay et al., 1983; Zhou et al., 2000). Coefficient of parentage was used for these comparisons; the relationships of a specific progenitor to its ancestors was set to zero before analysis so that the CP would directly estimate that progenitor's average genetic contribution (Gizlice et al., 1994).

As per Mikel and Kolb (2008), breeding progress was estimated by calculation of change per breeding cycle by comparing agronomic data of progeny and either of its cultivar parent(s) from the last cross before inbreeding. Agronomic data was obtained directly from U.S. utility patent, U.S. PVP, and USDA Uniform Soybean Tests for the Northern and Southern States, where both progeny and their parent(s) were evaluated in the same testing environments. Agronomic data were weighted by the number of environments contributing to the mean. SAS PROC GLM was used on the weighted means to test the null hypothesis that there was no significant difference between the overall progeny and parent agronomic means among all the registration comparisons where data were available (SAS Institute, 2007). Statistical significance of progeny–parent mean is determined as $P = 0.01$, $P = 0.05$, or not significant for each measured trait. The number of progeny–parent comparisons and number of environments contributing for each mean are shown. The following agronomic data were collected: seed yield (kilograms per hectare) at harvest, plant height (centimeters) measured as soil to top node of plant, plant lodging (rated 1 through 5, with 1 being least lodging), seed oil (percentage dry weight basis), seed protein (percentage dry weight basis), maturity date (harvest maturity as deviation of parent from progeny in days), seed size (grams per 100 seed), seed shatter (pod dehiscence before harvest rated 1 to 5, 1 is least pod shatter), and seed quality (1 to 5, 1 is best seed quality). SAS PROC CORR was used to calculate Pearson correlation coefficients for seed yield and diversity between parent and progeny versus the collected agronomic data previously described.

# RESULTS AND DISCUSSION

## Overview of Registered Cultivars

From 1970 to 2008 there were 2886 soybean cultivar registrations consisting of 1557 U.S. PVPs, 907 U.S. utility patents, and 422 cultivar journal registrations, respectively (Table 1). After accounting for cultivars that were registered by more than one media, there were 2242 nonredundant cultivar registrations. For example, it was common for public programs to register the same cultivar by both PVP and journal as well as for proprietary programs to register a cultivar by both PVP and utility patent. Plant Variety Protection became available in 1970 and patent registration of seed-propagated plants became available in 1985. The first soybean cultivars to be patented were ST1570 (9202709) and ST2550 (9211713) on 19 Apr. 1994 by Stine Seed Farms, Inc. (Eby, 1994a,b; Stine Seed Company, 2008).

Approximately 80% of cultivars registered from 1970 through 2008 were developed from proprietary programs and 20% from public institutions (Table 1). Registered cultivars were from: Monsanto, 25% of registered cultivars (through merger Asgrow Seed, Dekalb Genetics, Delta Pine and Land, and Monsanto); public institutions, 20%; Pioneer Hi-Bred, 17%; Syngenta, 12% (Advanta, Agripro Seeds, Northrup King, and Syngenta); Stine Seed and Monsanto jointly, 10% (Stine Seed Farms, Inc., joint patents with either Monsanto Technology or Asgrow Seed Company); and Midwest Oil Seeds–Stine Seed, 4%. The remaining 11% of proprietary cultivars were from 48 different originators. Those cultivars patented jointly by Stine Seeds with Monsanto (Asgrow) are facilitated by a nonexclusive collaboration between Monsanto and Asgrow Seed Company (subsidiary of Monsanto) and Stine Seed (Midwest Oilseeds) that began in 1997 (AFX News, 1997; Monsanto, 1997, Stine Seed Company, 2008).

Examination of recently (2004 to 2008) developed cultivars indicates far fewer originators (data not shown). These 482 cultivars were developed by: Stine Seed and Monsanto jointly, 35% of cultivars (168 cultivars); Pioneer Hi-Bred, 23% (109); Monsanto, 15% (70 from Monsanto, Delta Pine and Land, Asgrow Seed, and Dekalb Genetics); public programs, 9% (44); Stine Seed and Asgrow Seed jointly, 8% (37); Syngenta, 6% (30); Dairyland Seed, 2% (9); and other proprietary programs, 3% (15). Given that publicly originated cultivars are grown on a small percentage of farmers' fields, this indicates that the more recently developed North American commercial soybean cultivars originate largely from a small number of breeding programs. Most registered cultivars were from MG groups II, III, and IV (Table 2). Pubescence color was 64% tawny and 36% gray. More cultivars had tan (57%) than brown pod color (43%). Purple (63%) was more common than white (37%) flower color. Growth habit was 76% indeterminate, 23% determinate, and 1% semi-determinate. Herbicide resistance was not available until the last half of this era. Thus, 58% of the registered cultivars had no herbicide tolerance, 39% were glyphosate tolerant, and 3% had ALS tolerance. Of the 374 cultivars most recently registered (2005 through 2008), 87% were glyphosate tolerant, including 92% of proprietary cultivars (317) and 23% of publicly developed cultivars (7).

## Leading Germplasm in Breeding New Cultivars

To identify the predominant parental lines for breeding new cultivars during this era, the number of times a cultivar was used as a parent in the last cross before inbreeding was determined. Backcross-derived isolines were considered the same as the recurrent parent cultivar. The 10 most-used parental cultivars in crosses were Williams, A3127, Essex, Amsoy, Corsoy, Wayne, Forrest, Hutcheson, MO13404, and Bedford (Table 3).

The early (MG 00, 0, I, and II) maturities were predominantly 'Harosoy' derivatives (Table 4). Harosoy was used in developing breeding populations in the 1970s and the Harosoy progeny Amsoy, Corsoy, and Hark in the late 1970s and 1980s. The cultivars B216 and Hodgson derived from crosses made with Corsoy were popular as germplasm in the 1980s. In the late 1990s the Midwest Oilseeds cultivars MO61615 and MO01718, and later in the 2000s MO13404, were widely used. The cultivars Evans and P9061 were frequently used in developing new cultivars in MG 00 and

**Table 1. Originators of registered North American soybean [*Glycine max* (L.) Merr.] cultivars, 1970 to 2008.**

| Originator | No. cultivars registered by† | | | |
|---|---|---|---|---|
| | PVP | Patent | Journal | Unique cultivars‡ |
| Public Institutions | 420 | 7 | 396 | 438 |
| Pioneer Hi-Bred | 347 | 204 | | 380 |
| Asgrow Seed | 135 | 119 | 4 | 245 |
| Syngenta§ | 168 | 50 | 6 | 216 |
| Monsanto and Stine Seed jointly | | 168 | | 168 |
| Monsanto | 63 | 115 | | 167 |
| Midwest Oilseeds/Stine Seed | 4 | 95 | | 99 |
| Delta Pine and Land | 77 | 38 | 2 | 96 |
| Asgrow Seed and Stine Seed jointly | | 63 | | 63 |
| Dekalb Genetics | 48 | 26 | 2 | 55 |
| Advanta USA | 32 | 7 | | 39 |
| Soybean Research Foundation | 33 | | | 33 |
| Hartz Seed | 32 | | | 32 |
| FFR Cooperative | 27 | | | 27 |
| AgriPro Seeds | 24 | | | 24 |
| Dairyland Seed | 15 | 9 | | 24 |
| Terral Seed | 13 | | | 13 |
| Land O'Lakes | 12 | | | 12 |
| Lubrizol | 12 | | | 12 |
| Other Corporations¶ | 95 | 6 | 12 | 99 |
| **Total** | **1557** | **907** | **422** | **2242** |

†Registration through Plant Variety Protection (PVP), U.S. utility patent (Patent), or International Journal Publication (Journal).

‡Removes redundancy for cultivars registered by more than one media.

§Includes registered cultivars from Syngenta, Novartis Seeds, Northrup King, and Funk Seeds.

¶Consists of 41 proprietary originators each with fewer than 7 registered cultivars.

**Table 2. Phenotypic characteristics of soybean [*Glycine max* (L.) Merr.] cultivars registered from 1970 to 2008.**

| Characteristic | No. cultivars† | Percent |
|---|---|---|
| Pubescence color: | | |
| Gray | 806 | 36 |
| Tawny | 1413 | 64 |
| **Total** | **2219** | |
| Pod color: | | |
| Brown | 949 | 43 |
| Tan | 1258 | 57 |
| **Total** | **2207** | |
| Flower color: | | |
| Purple | 1398 | 63 |
| White | 814 | 37 |
| **Total** | **2212** | |
| Growth habit: | | |
| Determinate | 517 | 23 |
| Indeterminate | 1669 | 76 |
| Semi-determinate | 16 | 1 |
| **Total** | **2202** | |
| Herbicide tolerance: | | |
| Acetolactate synthase | 66 | 3 |
| Glyphosate | 866 | 39 |
| None noted | 1303 | 58 |
| **Total** | **2235** | |
| Maturity Group: | | |
| 00 | 22 | 1 |
| 0 | 160 | 7 |
| I | 265 | 12 |
| II | 509 | 23 |
| III | 450 | 20 |
| IV | 311 | 14 |
| V | 250 | 11 |
| VI | 147 | 7 |
| VII | 82 | 4 |
| VIII | 33 | 1 |
| IX | 4 | 0 |
| X | 2 | 0 |
| **Total** | **2235** | |

†Number cultivars where characteristic is noted.

MG 0. In MG I, the cultivars MO91133 and A1900 were popular parents. Maturity group II germplasm was largely derived from the Harosoy lineage through Amsoy, Corsoy, MO01718, MO13404, and Hark. MO61615 (Stine Seeds cultivar ST2250; Eby, 1999), an A3127 derivative, and its parent A3127 were important germplasm in MG II, with the use of A3127 extending into MG III and MG IV.

Williams and its derivatives were the main progenitors in the middle maturities. Chronologically, Wayne (Williams parent) was frequently used in crosses in the 1970s. Wayne was replaced in the 1980s by its progeny Williams. Of the many Williams first breeding cycle progeny, A3127 was widely used in the late 1980s and 1990s as a parent. A3127 is a proprietary cultivar developed by crossing Williams by Essex. Essex is a line from the cultivar Lee lineage that is representative in southern soybean germplasm. First cycle progeny of A3127 having the most impact on breeding programs in the 1990s were the cultivars MO61615, A2943, and P9273. Two widely used A3127 breeding cycle progeny were the cultivars P93B82, a direct progeny of P9273, and A3431, a direct progeny of A2943.

Progeny of the cultivars Lee and Bragg dominate later maturity groups. Lee and Bragg descended from the cross of S-100 × CNS. Lee was directly developed from this cross, and Bragg, indirectly, through the breeding line D49-2491. Lee and D49-2491 were both selected from the same F2 plant from S-100 × CNS (Sneller, 1994). Bragg contributed to crosses in the 1970s and 1980s and is a significant progenitor in the later maturity groups. The Bragg progeny 'Braxton' and Forrest were used as parents in the 1980s and 1990s. The Forrest progeny Bedford was popular germplasm in the 1980s and 1990s in MG VI. Lee was used in the 1970s and 1980s, and its progeny 'Pickett' and Essex in the 1980s and 1990s. The cultivar Centennial (Pickett progeny), the Essex lineage through Hutcheson, and 'A5403' contributed to southern germplasm in the 1990s.

The Williams derivative A3127 was the most used parent in proprietary breeding programs. In public breeding

Table 3. Soybean [*Glycine max* (L.) Merr.] varieties most used in breeding crosses for development of new cultivars, 1970 to 2008.

| Cultivar† | Pedigree | Notable public ancestor(s) | MG‡ | No. times used as parent in last cross before inbreeding | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | 1970–2008 | 1970–1979 | 1980–1989 | 1990–1999 | 2000–2008 |
| Williams | Wayne/L57-0034 | Wayne | III | 70 | 8 | 53 | 9 | |
| A3127 | Williams/Essex | Williams, Essex | III | 63 | | 34 | 28 | 1 |
| Essex | Lee/S55-7075 | Lee | V | 45 | 4 | 31 | 9 | 1 |
| Amsoy | Adams/Harosoy | Harosoy | II | 38 | 18 | 20 | | |
| Corsoy | Harosoy/Capital | Harosoy | II | 33 | 19 | 14 | | |
| Wayne | L49-4091/Clark | Lincoln | III | 30 | 21 | 9 | | |
| Forrest | Dyer/Bragg | Bragg | V | 27 | 2 | 19 | 6 | |
| Hutcheson | V68-1034/Essex | Essex | V | 25 | | | 18 | 7 |
| MO13404 | MO850126/MO63639 | Harosoy | II | 23 | | | | 23 |
| Bedford | Forrest *2//D68-18/PI88788 | Forrest | V | 23 | | 10 | 13 | |
| Beeson | C1253/Kent | Lincoln | II | 21 | 8 | 11 | 2 | |
| Hark | Hawkeye/Harosoy | Harosoy | I | 21 | 10 | 11 | | |
| Centennial | D64-4636/Pickett71 | Lee | VI | 20 | | 13 | 7 | |
| Bragg | Jackson/D49-2491 | D49-2491 | VII | 19 | 11 | 7 | 1 | |
| Calland | C1253/Kent | Lincoln | III | 19 | 8 | 11 | | |
| A5474 | Tracy/D71-6234//J74-122 | Forrest | V | 18 | | 2 | 16 | |
| A5979 | Young/A5474 | Essex, Forrest | V | 18 | | | 10 | 8 |
| MO61615 | A3127/MO11702 | Williams, Essex | II | 17 | | | 9 | 8 |
| P93B82 | P9273/3/XB33B//A3733/Resnik | Williams, Essex | III | 17 | | | | 17 |
| MO01718 | MO50321/MO50226 | Harosoy | II | 16 | | | 7 | 9 |
| Fayette | Williams *2 × PI88788 | Williams | III | 16 | | 1 | 15 | |
| P9061 | Wells/P1677 | Wells | 0 | 16 | | | 15 | 1 |
| Harosoy | Mandarin (Ottawa) 2*/A.K. (Harrow) | | II | 16 | 14 | 1 | | 1 |
| A2943 | A1564/A3127 | Williams, Essex | II | 15 | | 1 | 14 | |
| Davis | D49-2573/N45-1497 | Ogden, Roanoke | VI | 15 | 2 | 10 | 3 | |
| DP415 | Essex/DPX436 | Essex | V | 15 | | | 14 | 1 |
| Ransom | N55-5931/N55-3818//D56-1185 | Ogden, Roanoke | VII | 15 | 3 | 11 | | |
| Mack | NC55 *3/S62-5-16-12//RA63-19-2/3/ Lee 68 | Lee | V | 14 | 4 | 9 | | 1 |
| S19-90 | B152/Pella | Harosoy | I | 14 | | | 13 | 1 |
| Pella | L66L-137/Calland | Harosoy | III | 14 | | 7 | 7 | |
| A3431 | A2943/A5474 | Williams, Essex, Forrest | III | 13 | | | 10 | 3 |
| A4715 | A5474//Douglas/A3127 | Harosoy, Williams, Essex, Forrest | IV | 13 | | | 12 | 1 |
| B216 | Corsoy/Wayne | Harosoy, Wayne | II | 12 | | 12 | | |
| Hodgson | Corsoy/M372 | Harosoy | I | 12 | | 12 | | |
| Mitchell | Amsoy/Wayne | Harosoy, Wayne | IV | 12 | 2 | 9 | 1 | |
| P9273 | P2981/A3127 | Harosoy, Williams, Essex | II | 12 | | | 10 | 2 |
| Tracy | D61-618/D60-9647 | Bedford | VI | 12 | | 7 | 5 | |
| Cutler | C1069/Clark | Lincoln | IV | 12 | 7 | 5 | | |

†Cultivar notation and origin are as follow: Asgrow Seed (A), Delta Pine and Land (DP), Midwest Oilseeds–Stine Genetics (MO), Pioneer Hi-Bred (P), Syngenta Seeds (S). Public cultivars are recognized by standard designation (Bernard et al., 1988).

‡Maturity group.

programs, Williams (A3127 parent) was the most-used parental cultivar. Within Monsanto's germplasm, the five most-used cultivars in their breeding program were A3127 (used as parent 20 times), MO13404 (15), MO61615 (13), MO01718 (13), and A5979 (12). Monsanto southern germplasm is derived from A5979, Essex, and Hutcheson. Midwest Oilseeds cultivars, including MO61615, MO13404, and MO01718, were licensed to other seed companies for branding and commercialization.

Important germplasm within Pioneer's breeding program included P93B82 (used as parent 17 times) as middle maturity germplasm and P9061 (12) as early maturity germplasm. Syngenta benefited from the use of their proprietary cultivar S19-90 (10 parental crosses) in early MGs, and Essex (9) in late MGs. The most-used competitor cultivars in Syngenta's breeding program were A3127 (used as parent 9 times) and MO13404 (5). It is apparent that breeders

**Table 4. Number of times key progenitor cultivars used in last cross before inbreeding by maturity group.**

| | No. times used as parent of registered cultivars within MG† | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Cultivar‡ | 00 | 0 | I | II | III | IV | V | VI | VII | VIII |
| Hampton 266 | | | | | | | | 1 | 3 | 3 |
| Hutton | | | | | | | | 1 | 3 | 3 |
| Bragg | | | | | | | 2 | 3 | 10 | 4 |
| Lee | | | | | | | 2 | 4 | 1 | |
| DP415 | | | | | | | 9 | 4 | 2 | |
| Braxton | | | | | | | | 1 | 7 | 3 |
| Ransom | | | | | | | | 2 | 6 | 1 |
| Bedford | | | | | | 2 | 8 | 10 | 2 | 1 |
| Centennial | | | | | | | 2 | 10 | 6 | 1 |
| Pickett | | | | | | | | 8 | 5 | 1 |
| Hutchinson | | | | | | 3 | 15 | 5 | 1 | 1 |
| A5979 | | | | | | | 13 | 5 | | |
| A5403 | | | | | | | 11 | | | |
| Forrest | | | | | | 3 | 11 | 7 | 4 | 2 |
| Essex | | | | | 7 | 15 | 17 | 6 | | |
| A5474 | | | | 1 | 2 | 6 | 8 | 1 | | |
| A4715 | | | | | | 12 | 1 | | | |
| Mitchell | | | | | 2 | 10 | | | | |
| A3431 | | | | 3 | 9 | | | | | |
| Wayne | | | 3 | 9 | 11 | 7 | | | | |
| P93B82 | | | | 3 | 9 | 5 | | | | |
| A3559 | | | | | 8 | | | | | |
| Calland | | | | 7 | 8 | 4 | | | | |
| Williams | | | 3 | 9 | 40 | 15 | 3 | | | |
| Amsoy | | 1 | 5 | 18 | 3 | 4 | | | | |
| A3127 | | | 4 | 17 | 31 | 11 | | | | |
| P9273 | | | 1 | 5 | 6 | | | | | |
| MO13404 | | | 1 | 12 | 10 | | | | | |
| MO61615 | | | 3 | 14 | | | | | | |
| MO01718 | | 1 | 1 | 14 | | | | | | |
| A2943 | | | 1 | 7 | 6 | 1 | | | | |
| Beeson | | | 5 | 11 | 3 | 2 | | | | |
| S19-90 | | 1 | 5 | 8 | | | | | | |
| MO91133 | | 1 | 7 | | | | | | | |
| A1900 | | 1 | 7 | 2 | | | | | | |
| B216 | | 1 | 2 | 8 | 1 | | | | | |
| Corsoy | | 3 | 6 | 15 | 8 | 1 | | | | |
| Hark | | | 6 | 10 | 3 | 1 | | | | |
| Harosoy | | 2 | 6 | 4 | 3 | 1 | | | | |
| Hodgson | | 2 | 4 | 4 | 1 | 1 | | | | |
| Vinton | | | 6 | | | | | | | |
| P90B43 | | 5 | | | | | | | | |
| P9061 | 2 | 9 | | | | | | | | |
| Evans | 2 | 6 | | | | | | | | |
| Maple Ridge | 2 | | | | | | | | | |
| | Harosoy lineage§ | | | | | | | | | |
| | | | | Williams lineage | | | | | | |
| | | | | | | | | | | S-100 Lineage |

†Number of times cultivar was used as a parent in last cross before inbreeding in the development of cultivars within each maturity group.

‡Cultivar notation and origin are as follow: Asgrow Seed (A), Delta Pine and Land (DP), Midwest Oilseeds–Stine Genetics (MO), Pioneer Hi-Bred (P), Syngenta Seeds (S). Public cultivars are recognized by standard designation (Bernard et al., 1988).

§Predominant ancestral lineage grouping of cultivars within maturity groups.

have benefited from both germplasm from other programs as well as their own in-house proprietary germplasm.

Today, the elite commercial soybean cultivars are proprietary, and contemporary registration of new cultivars frequently includes utility patent protection. Breeders cannot use competitor cultivars without the originators' consent, and this restricts availability of germplasm between breeding programs. Proprietary germplasm registered by U.S. PVP and/or utility patent do eventually become available to the public on expiration of protection (Mikel, 2006). These soybean cultivars can be used without restriction for commercial production and/or breeding new cultivars. The caveat is that this germplasm is antiquated by several breeding cycles over the 15 to 20 yr of patent protection. This germplasm may offer future opportunities for developing new cultivars by intercrossing proprietary germplasm pools that are becoming isolated because of the restraints of utility patent protection.

## Types of Breeding Crosses and Methodology

During this era, soybean breeders used predominantly (70%) two-parent breeding crosses, followed by complex cross (12%), three-parent cross (5%), BC1 (5%), BC2 through BC4 (3%), BC5 and greater (2%), selection within a cultivar (1%), and both broad base and section mutation (less than 1%) (Table 5). There are several differences between public and proprietary breeding programs. First was the frequent use of two-parent crosses in public (81%) versus proprietary (67%) programs. Second, complex crosses were more common in proprietary (15%) than in public (2%) programs, which can be explained by the emergence in the middle 1990s of the transgene for glyphosate resistance. The Monsanto transformation event 40-3-2 of cultivar A5403 was the original glyphosate-resistant source released to licensees (Padgette et al., 1995). To meet market demand, it became imperative for proprietary programs to quickly introduce glyphosate-resistant commercial cultivars. The goal was not to create glyphosate-resistant isolines of existing cultivars. Rather, complex crosses and partial backcrosses into many commercial cultivars facilitated rapid transfer of glyphosate resistance into proprietary germplasm (Sneller, 2003). These complex crosses facilitated glyphosate-resistant conversions that were inbred to create many glyphosate-resistant cultivars. Concomitant with the increased use of complex crosses to introduce glyphosate resistance was decreased use of two-parent breeding crosses in proprietary breeding programs.

There was more use of breeding with multiple backcrosses to create isolines in the public than proprietary breeding programs. In proprietary programs, 1% of new cultivars originated from five or more backcrosses versus 5% in public programs. Backcrossing in public programs targeted the conversion of cultivars with genes conferring resistance to pathogens such as *Phytophthora sojae* Kaufmann and Gerdemann. Proprietary programs benefited from these isolines and used them as donors within their breeding programs.

Table 5. Types of soybean [*Glycine max* (L.) Merr.] breeding crosses used for development of North American cultivars registered from 1970 to 2008.

| | Overall | | Subdivided by decade | | | | | | | | Proprietary vs. Public derived | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1970–2008 | | 1970–1979 | | 1980–1989 | | 1990–1999 | | 2000–2008 | | Public | | Corporate | |
| Cross type† | No.‡ | Percent | No. | Percent | No. | Percent | No. | Percent | No. | Percent | No. | Percent | No. | Percent |
| 2-parent | 1322 | 70 | 134 | 74 | 319 | 75 | 515 | 65 | 354 | 74 | 352 | 81 | 970 | 67 |
| 3-parent | 103 | 5 | 11 | 6 | 29 | 7 | 44 | 6 | 19 | 4 | 9 | 2 | 94 | 7 |
| BC1 | 99 | 5 | 3 | 2 | 13 | 3 | 54 | 7 | 29 | 6 | 10 | 2 | 89 | 6 |
| BC2–BC4 | 63 | 3 | 8 | 4 | 18 | 4 | 27 | 3 | 10 | 2 | 27 | 6 | 36 | 2 |
| BC5+ | 32 | 2 | 12 | 7 | 14 | 3 | 6 | 1 | | 0 | 20 | 5 | 12 | 1 |
| Broad base | 9 | 0 | | 0 | | 0 | 2 | 0 | | 0 | 7 | 2 | 2 | 0 |
| Complex | 227 | 12 | 4 | 2 | 5 | 1 | 140 | 18 | | 0 | 8 | 2 | 219 | 15 |
| Mutation | 4 | 0 | 1 | 1 | 20 | 5 | 3 | 0 | 2 | 0 | 1 | 0 | 3 | 0 |
| Selection | 21 | 1 | 9 | 5 | 8 | 2 | 4 | 1 | 63 | 13 | 3 | 1 | 18 | 1 |
| **Total** | **1880** | | **182** | | **426** | | **795** | | **477** | | **437** | | **1443** | |

†Two-parent (2-parent), three-parent (3-parent), one backcross to recurrent parent (BC1), two to four backcrosses to recurrent parent (BC2–BC4), five or more backcrosses to recurrent parent (BC5+), broad base population, crossing involving more than three parents (Complex), induced mutation selection (Mutation), and selection within a cultivar (Selection).

‡Number of times breeding cross used in the development of new registered cultivars.

From 1970 through 2008, several specific crosses generated multiple registered cultivars (Table 6). The cross that generated the most cultivars was Williams × Essex. Over a 10 yr period, this two-parent cross generated 15 registered soybean cultivars ranging from MG III through V, with the most notable being A3127. Of these 15 cultivars derived from Williams × Essex cross, many were attempts to resample the genetic potential that generated A3127. However, all seven of the Asgrow cultivars listed in Table 6 from this cross were developed simultaneously beginning with the same initial cross in 1972 (Plant Variety Protection Certificates 7700096, 7700100, 7700101, 7700111, 8000086, 8100084, and 8300139). This cross resulted in a large number of commercial cultivars ranging from MG III through MG V that were widely geographically adapted.

## Estimation of Genetic Diversity

Genetic diversity measured as pedigree diversity is 0.89 among registered soybean cultivars developed from 1970 through 2008 (Table 7). Diversity was the same within public (0.89 among 434 cultivars) and proprietary (0.89, 1449) germplasm.

Table 6. Most-used breeding populations for development of soybean [*Glycine max* (L.) Merr.] cultivars registered from 1970 to 2008.

| No. cultivars† | Pedigree‡ | Notable public ancestor(s) | MG§ | Year registered | First breeding cycle progeny¶ |
|---|---|---|---|---|---|
| 15 | Williams/Essex | Williams, Essex | III to V | 1977 to 1987 | A3127, A3659, A3860, A3966, A4268, A5308, A5312, B335, Co393, P9441, P9471, Pennyrile, RA452, RA481, S42-40. |
| 8 | Wayne/Hark | Wayne | I to IV | 1975 to 1982 | Classic1, DSR171, DSR207, DSR227, DSR232, DSR320, S1474, Stevens |
| 6 | Hutcheson/A5403 | Lee, Essex | V | 1996 to 2001 | A5547, A5843, A5944, M8816075696, M8967515073, Caviness |
| 6 | Amsoy/Corsoy | Harosoy | II to III | 1978 to 1981 | Amcor, GL2250, Gutwein221, Matsoy, PL723299L, PL72-3176L |
| 5 | 851008/Midwest Oil expt 895325 | Harosoy, Williams, Essex | III | 1998 | M3460606, M3539836, M34606, M34606S5, M35398S5 |
| 5 | A3127/Williams82 | Williams, Essex | II to III | 1986 to 1990 | A3501, A3511, CX298, CX329, GR8936 |
| 5 | DP415/A5980 | Essex, Lee | V | 1993 to 1995 | DP3553, DP3588, DP3589, TV5495, TV5555 |
| 5 | CX458/CX366 | Williams, Essex | III to IV | 1994 | CX335, CX377, CX399, CX411, CX434 |
| 5 | Williams/Ransom | Williams, Lee | II to IV | 1980 to 1982 | Elf, Gnome, Hobbit, Hobbit, Sprite |
| 5 | Corsoy/Wayne | Harosoy, Wayne | I to III | 1975 to 1984 | B186, B216, Riverside2024, S1244, S1492 |
| 5 | MO01336 *2/MO71005-05RR | Williams, Essex | 0 to II | 1999 to 2000 | MO61623474, MO61630497, MO61631202, MO63048123, MO163049318 |

†Number of cultivars registered derived from this breeding cross.

‡Cultivar notation and origin are as follow: Asgrow Seed (A prefix), Coker (Co), Dekalb (CX), Delta Pine and Land (DP, SG), Dairyland Seed (DSR), Monsanto (M), Pioneer Hi-Bred (P), Ring Around Products (RA), Soybean Research Foundation (GL, PL), Syngenta Seeds (B, S), and Terral Seed (TV). Public cultivars are noted with standard designation (Bernard et al., 1988).

§Maturity group.

¶Registered cultivars derived from this breeding cross (pedigree).

**Table 7. Progenitors of 494 proprietary soybean [*Glycine max* (L.) Merr.] cultivars registered from 1999 to 2008.**

| Progenitor† | No. descendents with a genetic contribution of 25%‡ |
|---|---|
| A3127 | 117 |
| P9273 | 57 |
| Williams | 50 |
| Lincoln | 45 |
| MO13404 | 36 |
| P93B82 | 34 |
| A5474 | 33 |
| A5979 | 23 |
| Essex | 23 |
| P9061 | 23 |
| MO061615 | 22 |
| MO01718 | 19 |
| A2943 | 19 |
| Forrest | 12 |
| S19-90 | 11 |
| Wayne | 9 |
| Harosoy | 8 |
| Corsoy | 5 |
| Lee | 2 |
| D49-2491 | 0 |

†Cultivar notation and origin are as follow: Asgrow (A), Midwest Oilseeds–Stine Genetics (MO), Pioneer Hi-Bred (P), and Syngenta Seeds (S). Public cultivars are recognized by standard designation (Bernard et al., 1988).

‡Number of proprietary cultivars registered from 1999 through 2008 that are descendents of progenitor cultivar with a genetic contribution of 25% from the progenitor. The genetic contributions from these progenitors are not independent owing to redundancy within lineages.

Our estimate of pedigree diversity (0.89) for 1883 registered soybean cultivars was similar to Sneller's (1994) estimate of 0.83 for a select smaller group of 122 soybean lines developed before 1994. Pedigree-based genetic diversity estimates for other self-pollinated crops such as barley (*Hordeum vulgare* L.) range from 0.81 to 0.93 (Martin et al., 1991; Mikel and Kolb, 2008). Diversity for wheat (*Triticum aestivum* L.) ranges from 0.78 to 0.91 (Almanza-Pinzon et al., 2003; Sud et al., 2005; Van Beuningen and Busch, 1997). Pedigree diversity for cotton (*Gossypium hirsutum* L.) varied from 0.80 to 0.88 (Van Esbroeck et al., 1998). Slightly more diversity (0.94) was found in rice (*Oryza sativa* L.) than the other self-pollinated crops (Wang and Lu, 2006). Mikel (2008) estimated genetic diversity in North American dent corn as 0.94 for all registered inbred lines from 1976 to 2005. One caveat exists for pedigree-based estimates of genetic diversity, because any parents or ancestors with unknown parentage contribute to increasing diversity. This is true for this work and pedigree-based estimates for the diversity of other crops that have been previously used for comparison in this discussion.

Overall, genetic diversity appears similar across field crops. It is difficult to estimate soybean diversity in farmers' fields, because farmers largely grow proprietary cultivars. For proprietary germplasm, there is little information on the production of cultivars regionally, nationally, or internationally. Mikel (2008) estimated that diversity was 0.86 among 47 widely grown North American dent corn hybrids of the era 1995 to 2001. Genetic diversity estimates for 69 registered (1970 to 2006) malt barley cultivars was 0.89, but for a subset of the 15 most widely (2001 to 2005) grown, diversity was lower, at 0.78 (Mikel and Kolb, 2008). It is understandable that diversity decreases as focus shifts to a subset of cultivars adapted for a geographical area or era of time. Generally, plant breeders recycle the most elite cultivars to develop new cultivars. Frequently, this involves the recombination of a small set of closely related cultivars as seen with barley and within inbred heterotic groups in dent corn. (Mikel and Kolb, 2008; Mikel 2008; Mikel and Dudley, 2006).

Estimates of genetic diversity within proprietary (0.89) soybean cultivars was the same as for public (0.89) cultivars. This is not surprising in view that both public and proprietary breeders both initially had access to the same public cultivars. Genetic diversity was 0.89 for public, 0.90 for Monsanto, 0.83 for Pioneer Hi-bred, 0.89 for Syngenta, and 0.87 for cultivars from other companies. Genetic diversity was similar within these sources of germplasm. Monsanto, through acquisition and germplasm collaboration with Stine Seed, has access to a large germplasm source, but overall diversity within this germplasm was similar to the other sources.

For cultivars registered from 1970 to 2008, pedigree diversity by maturity group was 0.83 (MG 00, 21 cultivars), 0.86 (MG 0, 122), 0.85 (MG I, 203), 0.87 (MG II, 411), 0.80 (MG III, 378), 0.83 (MG IV, 259), 0.83 (MG V, 233), 0.83 (MG VI, 146), 0.78 (MG VII, 80), and 0.78 (MG VIII, 33). The reduced diversity observed in MG VII and MG VIII compared with earlier MGs is largely the result of fewer cultivars as well as prevalence of the S-100 (D49-2491 and Lee) lineage in the development of these later maturity cultivars. Diversity was maintained in the early maturity groups despite being constituted by a small number of cultivars. The reduction of diversity in MG III is largely because of the wide use of Williams and its progeny in breeding new cultivars.

Genetic diversity was similar within northern (MG I, II, III; diversity 0.86) and southern (MG IV, V, VI; diversity 0.87) germplasm. Sneller (1994) found slightly more diversity (0.77) within northern (MG I, MG II, and MG III) than diversity (0.74) in southern (MG IV, V, and VI) cultivars. Factors contributing to these differences include two breeding cycles (14 yr between studies) and the much larger pool of cultivars (1658 cultivars in MG I through MG VI) sampled in this study versus Sneller (122 cultivars in MG I through MG VI). The prevalence of Williams and its progeny contributes to lowering diversity in northern germplasm. In addition, the "genetic bridge" between the northern and southern germplasm pool mentioned by Sneller (1994) has continued, with private industry breeding between the two germplasm pools.

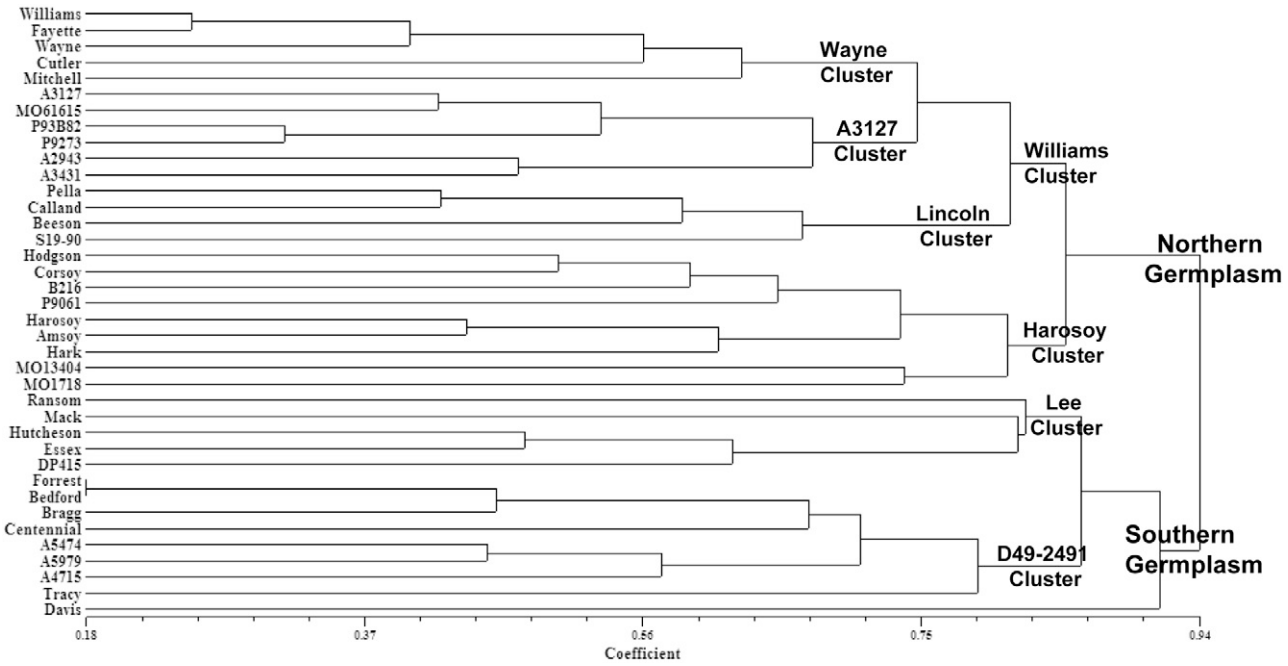


Fig. 1. Genetic distance of 38 prominent soybean [*Glycine max* (L.) Merr.] cultivars in breeding new cultivars.

Cluster analysis was used to group by genetic distance the 38 cultivars identified as key germplasm (Table 3) during this era (Fig. 1). There are two predominant divisions representing northern and southern germplasm. The northern group consists of the Williams and Harosoy clusters. The Williams cluster consists of three groups: Wayne, A3127, and 'Lincoln'. There have been many cultivars developed from interbreeding within the Williams cluster. Cultivars within the Williams groups are related through the progenitor Lincoln. The A3127 group represents a recently established germplasm pool derived from crosses between northern and southern germplasm. A3127 is a direct progeny of Williams, and the cultivars in its cluster are all direct progeny of A3127. Harosoy represents the second cluster of the northern germplasm. Harosoy cultivars are generally earlier maturity than those in the Williams cluster. The cultivars MO13404 and MO1718 fit into the Harosoy cluster but are less related to the other cultivars.

Southern germplasm consists of two clusters derived from the founder S-100, which is a direct parent of both Lee and D49-2491. The cultivar Davis only loosely fits into the D49-2491 cluster owing to diversity from 'Nanking' (through Roanoke) as well as 'Tokyo' and PI 54610, both from 'Ogden'. Thus, Davis has the most diversity among these southern cultivars in the D49-2491 cluster.

## Genetic Composition of Contemporary Proprietary Cultivars

In Table 7, the genetic contributions of key progenitors for 494 proprietary cultivars registered from 1999 through 2008 are shown. In some cases there is redundancy from several of the progenitors being in the same pedigree lineage. However, this does furnish an excellent overview of the composition of the more recently registered cultivars from the last 10 yr of this study. The impact of A3127 on today's germplasm is noteworthy. The cultivar A3127 has a genetic contribution of 25% or greater in 117 (23%) of these 494 contemporary cultivars. Furthermore, 247 (50%) of these cultivars have a genetic contribution of 10% from A3127. This shows that A3127 was not only an excellent direct parent, but its contribution has continued through multiple breeding cycles. Williams (parent of A3127) and P9273 (descendent of A3127) were also major contributors in the middle maturity groups. Contemporary early maturity group cultivars were impacted by the progenitors MO13404, P9061, A2943, and S19-90. Later maturity group germplasm had large genetic contributions from A5474, A5979, Essex, and Forrest.

## Evaluation of Breeding Progress

Direct agronomic comparisons of parent (of the last cross before inbreeding) and progeny furnish meaningful metrics to determine breeding progress. This provides an estimate of breeding gain under the cultural conditions at the time the cultivars are developed. Multiple comparisons over numerous environments, maturity groups, and crosses were found to estimate gain per breeding cycle. Seed yield was significantly increased by 3.2% per breeding cycle as measured from 208 crosses and 6321 environments (Table 8). By comparison, grain yield in barley increased by a greater rate of 4.4% per breeding cycle over roughly the same era (Mikel and Kolb, 2008). Grain yield of inbred dent corn (1976–2005) increased 6%, and hybrid grain yield (1995–2001) increased 2.2% per breeding cycle (Mikel, 2008). Unfortunately these breeding gains cannot

Table 8. Direct side-by-side agronomic comparisons between soybean [*Glycine max* (L.) Merr.] cultivars and their parents.

| Agronomic measurements | Parent† | Progeny | Percent of parent | *P*‡ | No. comp.§ | No. env.¶ |
|---|---|---|---|---|---|---|
| Seed yield (kg/ha)# | 3115 | 3214 | 103.2 | 0.01 | 208 | 6321 |
| Plant height (cm)†† | 35.1 | 34.8 | 99.1 | ns | 201 | 5061 |
| Plant lodging rating (1 to 5 scale, 1 is least lodging) | 2.1 | 2.0 | 95.2 | ns | 191 | 4575 |
| Seed oil (percentage dry weight basis) | 20.8 | 21.0 | 101.0 | ns | 125 | 1700 |
| Seed protein (percentage dry weight basis) | 40.9 | 40.6 | 99.3 | 0.01 | 127 | 1727 |
| Maturity date (days deviation from progeny)‡‡ | –0.6 | 0.0 | 100.6 | 0.01 | 190 | 4704 |
| Seed size (g/100 seed) | 15.9 | 15.8 | 99.4 | ns | 104 | 2277 |
| Seed shatter (1 to 5 scale, 1 is least shatter)§§ | 1.9 | 1.5 | 78.9 | 0.01 | 54 | 431 |
| Seed quality (1 to 5 scale, 1 is best quality)¶¶ | 2.0 | 2.0 | 100.0 | ns | 64 | 2525 |

†Comparison of progeny and their direct cultivar parent(s) from the last breeding cross before inbreeding. Parent and progeny were evaluated in side-by-side comparisons in the same environments.

‡Statistical significance at $P = 0.01$, $P = 0.05$, and not significant (ns).

§Number of different parent to progeny comparisons in the mean.

¶Number of environments in the mean.

#Seed yield at harvest.

††Plant height measurement is taken from the top of the soil to the top node of the plant.

‡‡Maturity is expressed as deviation of parent from progeny in days to maturity. Maturity is when 95% of the pods have reached their mature color.

§§Seed shatter is the amount of pod dehiscence before harvest.

¶¶Seed quality rating estimates quality based on wrinkling, defective seed coat, greenish or diseased seeds.

be readily compared among crops on a year basis because the number of years per breeding cycle is difficult to determine from the PVP, patent, and journal registrations.

Progeny had significantly less seed shatter than their parents, which contributed to increased yield per breeding cycle. Developed progeny were approximately a half day later in maturity than their parents. There was a significant reduction of seed protein per breeding cycle and a small, though not significant, increase of seed oil. Other agronomic traits such as plant lodging and seed quality were not significantly changed.

A significant correlation was found between seed yield gain per breeding cycle and diversity between progeny and parent (0.29). There was no correlation found between yield gain per breeding cycle and year of registration, suggesting that breeding progress for yield has not changed over this era.

## CONCLUSIONS

Soybean breeders have been effective in increasing seed yield. Overall, genetic diversity of soybean across maturities is similar to other field crops despite the popularity of recycling related elite cultivars. The cultivar A3127 and its progeny were aggressively recycled and make a genetic contribution of greater than 25% in 23% of the proprietary cultivars released between 1999 and 2009. Diversity is likely to be less in farmers' fields as a result of the use of a smaller subset of often closely related commercial cultivars. Other factors impacting genetic diversity are reduced presence of public breeding programs and consolidation of proprietary programs through corporate mergers. Current North American elite commercial soybean germplasm is largely from a small number of proprietary programs. This coupled with restrictions placed on germplasm by U.S. utility patents creates a small number of isolated breeding programs to meet the challenges for continual genetic improvement.


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